Journal of the Geological Society, London, Vol. **152,** 1995, pp. 407–413, 4 figs, 1 table. Printed in Northern Ireland

The discovery of a new Devonian tetrapod trackway in SW Ireland

I. STÖSSEL

Geological Institute, ETH-Zentrum, CH-8092 Zürich, Switzerland

Abstract: A tetrapod trackway has been discovered in Devonian sedimentary rocks of SW Ireland. It is the first discovery of its kind in Europe. Details of the footprints are not preserved, probably because of strong Variscan pressure solution cleavage. However, after removing the effect of Variscan deformation, the large number of footprints (more than 150) makes it possible to calculate the original dimensions of the footprint pattern: stride (approximately 34 cm) and pace (approximately 35 cm). These values are higher than those for other traces of comparable age. The total length of the tetrapod is estimated to be 1 m. Lithostratigraphical and biostratigraphical arguments indicate an age of Mid- to Late Devonian.

Keywords: Devonian, Old Red Sandstone, tetrapods, tracks, fluvial environment.

Trackways of Devonian tetrapods are very rare, but provide valuable insights into the earliest phase of the conquest of land by vertebrates. Only four finds have been reported until now. The oldest occurs in a pavement block in west Victoria, Australia (Warren *et al.* 1986), and consists of several footprints without any details. The suggested age of latest Silurian to earliest Devonian is based partly on radiometric data. Significantly younger is *Notopus petri* Leonardi from the Paraná Basin, Brazil, with an age near the Mid- to Late Devonian boundary. It is a single left manus (hand) imprint showing, in outstanding detail, a tetradactyle foot structure. This is the only Devonian imprint which has been described systematically (Leonardi 1983). A discovery of comparable age (earliest Late Devonian) from Victoria (Warren & Wakefield 1972) comprises three different trackways on a single bedding plane, and is the most extensive and most important fossil of its kind. One of these trackways shows pentadactyle impressions. The fourth record of Devonian trackways is an old one (found *c.* 1929) of which nothing but a sketch exists today (Sarjeant 1974). According to Leonardi (1983), this trackway may be the trace of a rhipidistian fish rather than the trackway of a real tetrapod.

More attention has been paid to the few Devonian tetrapod body fossils that are known (Lombard & Sumida 1992; Ahlberg & Milner 1994). The oldest bones in continental sediments (earliest Late Devonian) have been reported from Australia (Campbell & Bell 1977), the former USSR (Lebedev 1984, 1990; Lebedev & Clack 1993) and Scotland (Ahlberg 1991). These finds indicate considerable diversity and wide distribution of tetrapods by earliest Late Devonian time. The best known Devonian tetrapod fauna is that from the Famennian of East Greenland. The primitive amphibians *Ichthyostega* and *Acanthostega* are its famous representatives (Jarvik 1955, 1980; Clack 1988).

In 1992, a new, unusually extensive tetrapod trackway was discovered in Devonian sedimentary rocks of SW Ireland (Stössel 1993). Details of the footprints have been lost because of a strong Variscan pressure solution cleavage. However, the large number of footprints makes it possible to calculate the original dimensions of the footprint pattern. In this paper, an analysis of the trackway is presented.

Geological setting

The trackway is situated on the northern coast of Valentia Island, SW Ireland (Fig. 1). Due to erosion by Atlantic storms, the trackway is superbly exposed, and the site is easily accessible.

The geology of SW Ireland is dominated by the fill of the Mid- to Late Devonian Munster Basin (Capewell 1965), consisting of fluvial molasse sediments derived from the Caledonide mountains to the north. Following the British nomenclature, these post-Caledonide continental sediments are regarded as part of the Old Red Sandstone magnafacies (Williams *et al.* 1989). On the Atlantic coast of the Iveragh Peninsula (Fig. 1), three formations are recognized within the fluvial succession: from bottom to top, these are the Valentia Slate Formation, the St. Finan's Sandstone Formation, and the Ballinskelligs Sandstone Formation (Capewell 1975). Each of these formations is regarded as representing a vertical accumulation in a non-channelized alluvial plain (Graham 1983). The tetrapod trackway occurs in the Valentia Slate Formation, which consists mainly of fine-grained sandstones and siltstones of purple to purplish-grey colour.

The Variscan orogeny shortened the formerly extensional Munster Basin by approximately 50% in a NNW direction, mainly by regional folding, thrusting and cleavage development (Cooper *et al.* 1986). The intense cleavage strongly affected the trackway. However, it is possible to calculate the amount of cleavage strain in this particular case. The area was also affected by Variscan lower greenschist-facies metamorphism (Avison 1984). In the clastic sedimentary rocks, the metamorphism is evident from alterations of clay minerals and mica.

Description

The trackway follows a meandering path across a subhorizontal, partly rippled bedding plane of some 7 m by 10 m. This is the upper surface of an approximately 2 cm thick graded sandstone to siltstone bed (Fig. 2). One end of the track has been eroded; the other end disappears below the overlying sandstone bed. Some 150 footprints (concave epireliefs) are exposed, many of them infilled with sediment of the overlying bed. The footprints have a maximum depth of some 2 cm.

The trackway is incomplete in places (Fig. 2), either because the sediment was too hard during track formation, or because of penecontemporaneous erosion. It is impossible to distinguish these two effects today. Perhaps for these reasons, and also because of strong deformation, no

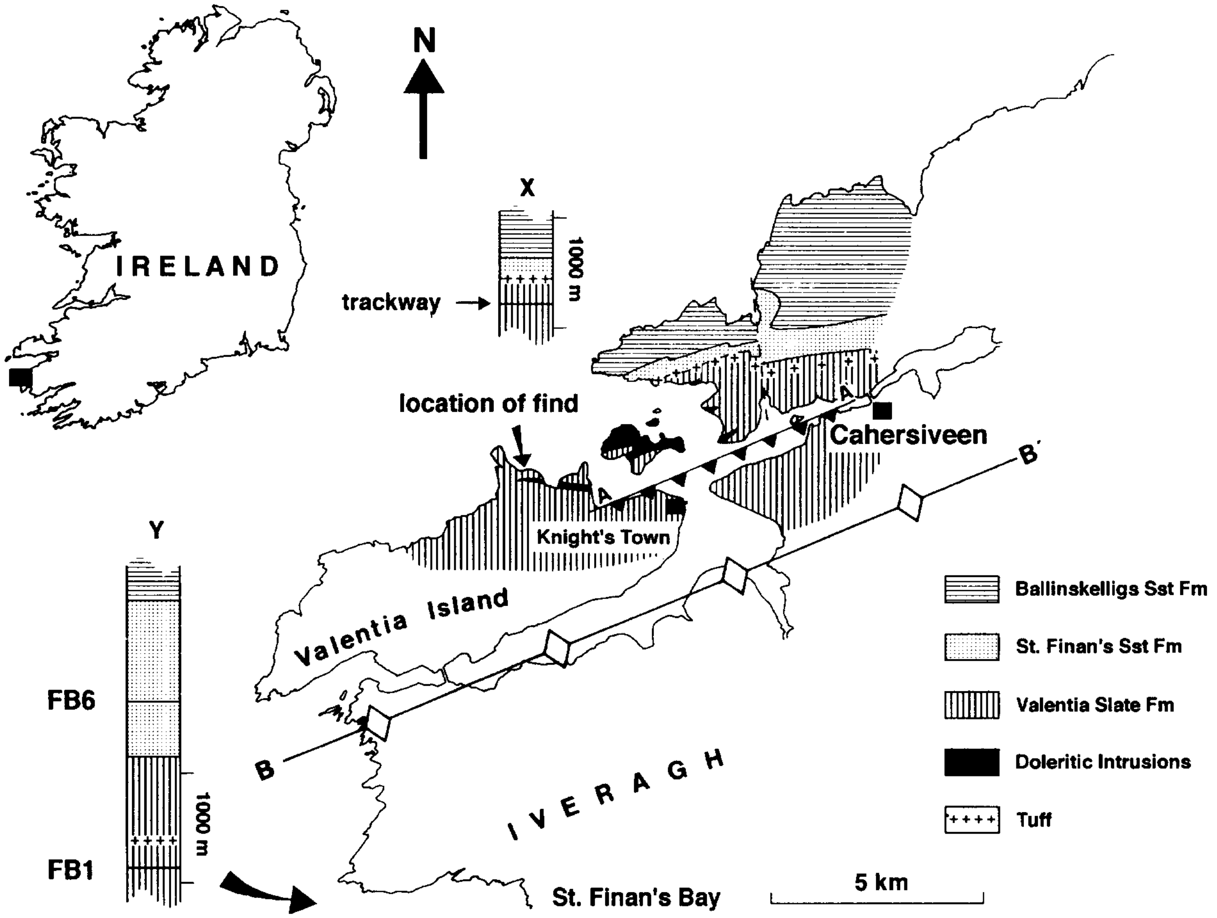

Fig. 1. Simplified geological map of the area surrounding the site of the trackway, based on Russell (1978, 1984) and Stössel (1993). X, Lithostratigraphy of the Valentia Harbour area, based on Stössel (1993); Y, lithostratigraphy of St. Finan's Bay area, based on Russell (1978, 1984); A-A′, Coomnacronia Fault; B-B′, Portmagee Anticline; FB1, fish-bed number 1; FB6, fish-bed number 6.

details of the individual footprints are preserved. Only one of them shows some kind of rough bilobate structure, which could be due either to foot morphology or to forward dragging of the foot. Both interpretations would indicate a movement direction from northeast to southwest. More information might be obtained by excavation of the infilled footprints.

There are two types of footprints which differ in size and which alternate systematically (Fig. 2). The smaller prints probably represent manus (=hand) impressions. The larger ones may thus represent the pes (=foot) impressions, and show a smaller width of pace (Fig. 3). Typically, the pes has not stepped onto the imprints of the manus, but sometimes the pes impression is placed immediately in front of the impression of the manus. The methodology of Peabody (1959) allows the estimation of the coupling value (a number derived by dividing body length by the sum of the lengths of forelimb and hindlimb) by comparing the trackway pattern with tracks of modern amphibians with known coupling values. This yields a value of 1.2 to 1.4.

Age

The Old Red Sandstone of SW Ireland is very poor in fossils (Higgs & Russell 1981 and references therein; O'Sullivan *et al.* 1986). Dating of the strongly oxidized sedimentary rocks, which contain diachronous facies boundaries, is therefore very difficult. Unfortunately, neither the base nor the top of the Valentia Slate Formation are exposed on Valentia Island itself. However, an approximately 1 m thick layer of fine-grained tuffaceous conglomerate, which is believed to be a distal equivalent of the Bealtra Agglomerate (Capewell 1975; Stössel 1993) exposed on the adjoining headland, allows the lithostratigraphical position of the tracks to be determined. The volcaniclastic rocks themselves lie below a tuff bed of regional extent (Enagh and Keel Tuff of Russell 1984). The track is estimated to lie some 230 m stratigraphically below this tuff bed. There are only two sets of biostratigraphical data which are of importance for the trackway: fish fossils found at St Finan's Bay (Russell 1978), a few kilometres south of the trackway site (Fig. 1), and a miospore assemblage found at Moll's Gap, some 50 km southwest of the site (Higgs & Russell 1981). Two fish-beds (FB1 and FB6 of Russell 1978) must be considered. FB6 definitely lies above the tuff bed, and therefore above the trackway. Russell (1978) suggested a Famennian age for this bed, based on remains of the genus *Sauripterus*.

If a constant rate of sediment accumulation is assumed, the bed bearing the tetrapod trackway would lie some 40 m stratigraphically above FB1 in the St Finan's Bay section. However, there is strong evidence for an increase in

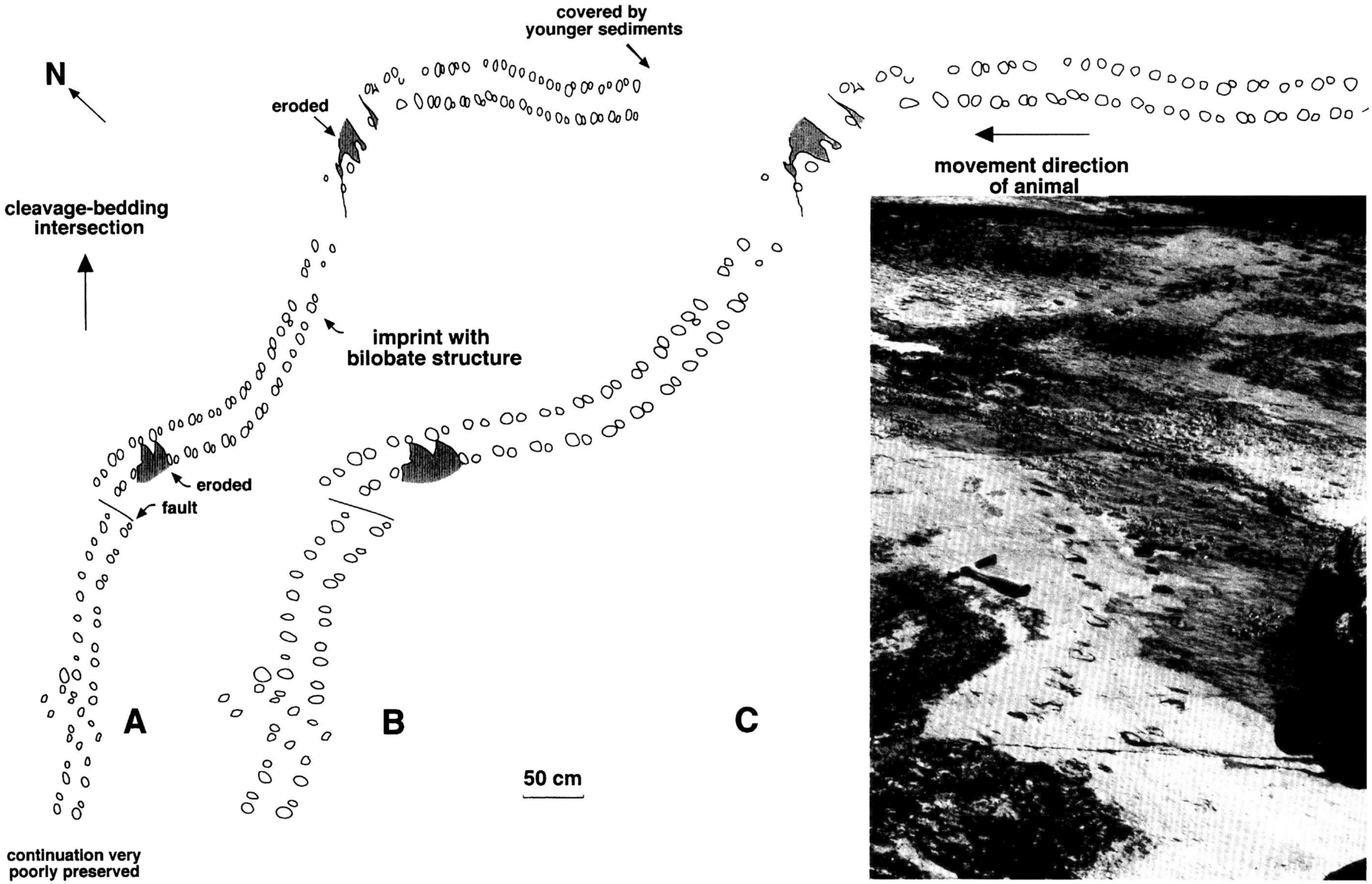
N
cleavage-bedding intersection
eroded
covered by younger sediments
imprint with bilobate structure
eroded
fault
continuation very poorly preserved
A
B
C
50 cm
movement direction of animal

Fig. 2. Original (**A**) and restored (**B**) plan view of the trackway. (**C**) shows part of the trackway, seen from northwest. Movement direction of the animal is towards the lower left corner. 50 cm scale applies to A and B.

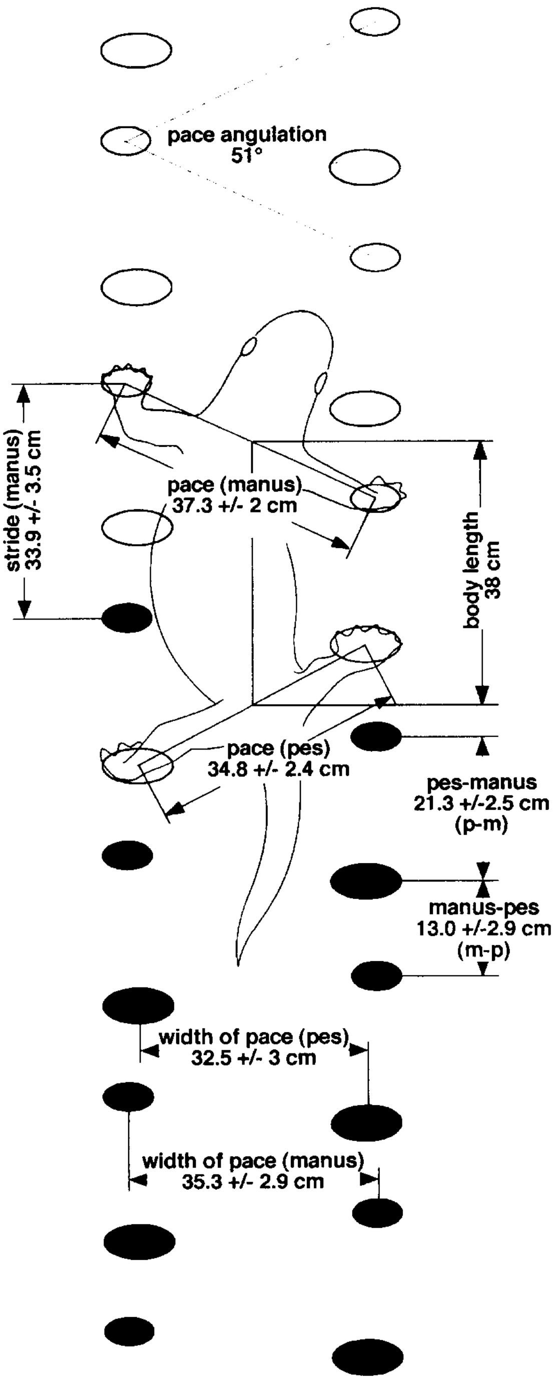

Fig. 3. Reconstruction of an 'ideal' trackway (based on calculated deformation parameters). The figure also attempts to show the gait of the animal and its probable dimensions.

sediment thickness from north to south, controlled by the Coomnacronia Fault (Capewell 1975; Stössel 1993; Fig. 1). Therefore, FB1 could theoretically lie stratigraphically above the trackway horizon. FB1 bears fossils of the genus *Bothriolepis*, which unfortunately has a very long range from Eifelian–Givetian to Strunian (Westoll 1979). So for FB1 a maximum age of Eifelian must be assumed.

The miospores of Moll's Gap, which give an early Frasnian age (Van Veen & Van Der Zwan 1980; Higgs & Russell 1981), occur in the Green Sandstone Formation which is thought to be a more proximal equivalent of the St. Finan's Sandstone Formation (Williams *et al.* 1989). Assuming isochronous facies boundaries, the trackway would lie well beneath the miospores. However, as the facies boundaries are unlikely to be isochronous which is indicated by the tuff bed, any correlation between the trackway and the miospore date is speculative. It would be very useful to find the equivalent of the tuff bed in eastern Iveragh.

In conclusion, the age of the trackway must lie between the age of the oldest rocks exposed in the Munster Basin, believed to be Mid-Devonian (Horne 1974; Williams *et al.* 1989), and the Famennian of FB 6.

Strain analysis

Southern Ireland lies within the Rhenohercynian zone of the Variscan Orogen (Rast 1983 and references therein), i.e. in the northern external zone, where cleavage development, folding and thrusting occurred during deformation (Cooper *et al.* 1986). The trackway is on the southern limb of a mesoscopic anticline which has a wavelength of several hundred metres, and in which the rocks are affected by an axial planar, pressure solution cleavage. A more or less systematic variation of stride, pace and width of pace in the trackway make it easy to recognize the influence of the strong cleavage strain at first sight (Fig. 2A). Assuming that the animal moved with constant speed and equal gait but varying direction, it is possible to analyse the strain using these parameters (Appendix). However the following restrictions must be kept in mind: (i) the absolute volume loss is unknown, (ii) a determinable strain ellipse is a two dimensional section of a three dimensional strain ellipsoid, and (iii) there is no information about the third dimension of this ellipsoid (except for direction of maximum shortening, which may be perpendicular to cleavage).

These three restrictions make it impossible to calculate anything other than ratios. However, if it is assumed that there was no significant extension parallel to the fold axis, it is possible to calculate the original dimensions of the footprint pattern. This assumption seems reasonable, as no stretching lineations have been found within the Irish Variscan fold belt (Bamford & Ford 1990). The maximum elongation on the bedding plane of the strain ellipse is chosen as a reference, i.e. dimensions parallel to fold axes are assumed to be unstrained.

In order to analyse the total strain, the following dimensions and corresponding azimuths were measured: pace, stride, width of pace for manus and pes, and the distances between manus and pes impressions (Fig. 3).

These values describe a strain ellipse which can be calculated as a best-fit ellipse using the method of minimal quadratic deviation (see Appendix). The following parameters were obtained (in relation to the subhorizontal bedding plane):

direction of shortening: N317°E

axial ratio of the ellipse (= 18.7/35.5) giving a shortening of approximately 47%.

In order to control these results, the amount of strain was also calculated using the range of the variation of deformed pace angulation (Ramsay & Huber 1983). However the higher the variation in the initial pace angulation, the higher will be the variation in the deformed pace angulation. Therefore this method yields a maximum shortening of 53%, which is close to the calculated shortening of *c.* 47%.

Using these deformation parameters, the original dimensions were calculated. The maximum value of 53% yields much bigger errors (calculated as standard deviation σ) than the value of 47%. Therefore only the latter value (47%) was used for further calculations of the dimensions of the track array. These give the following averages:

Pes:	pace:	34.8 cm; $\sigma = 2.4$ cm
	stride:	34.2 cm; $\sigma = 4.2$ cm
	width of pace:	32.5 cm; $\sigma = 3.0$ cm
Manus:	pace:	37.3 cm; $\sigma = 2.0$ cm
	stride:	33.9 cm; $\sigma = 3.5$ cm
	width of pace:	35.3 cm; $\sigma = 2.9$ cm
distances manus–pes (Fig. 3):		
	manus–pes (m-p)	13.0 cm; $\sigma = 2.9$ cm
	pes–manus (p-m)	21.3 cm; $\sigma = 2.5$ cm

The restored trackway is shown in Fig. 2B.

Obviously, the ellipticity of the footprints is not constant. There seems to be a systematic variation in relation to the movement direction, for which there are two possible reasons: either the deformation was very heterogeneous; or the footprints were originally not circular but elliptical in shape. The first possibility seems to be unlikely, for the calculated strain ellipse is very regular. The second possibility allows the determination of the original ellipticity of the footprints using the R_f/ϕ method (Ramsay & Huber 1983). This gives an approximate original ellipticity for the footprints (R_i) of 1.5.

Discussion

In order to compare the new trackway with those previously described, all significant data are compiled in Table 1.

The single find of *Notopus petri* Leonardi has an oval outline (Leonardi 1983). The size (71 × 60 mm) is slightly larger than the manus impression of the Irish trackway, but the ratio of length/width is of the same order. The possible bilobate footprint in the Irish trackway might have been produced by digit divarication, similar to that between digits III and IV (84°) of *Notopus petri*, but a direct morphological comparison is impossible.

The various tracks recorded by Warren & Wakefield (1972) do not show any preservation of the detailed morphology of the feet, except for their trackway I which has pentadactyle impressions. As indicated in Table 1, pace and stride are generally smaller than in the Irish trackway, even allowing for the possibility of limited extension parallel to the fold axis. The pace angulation of their trackway I is very similar to that calculated for the Irish trace (pace angulation is not very distinctive as it changes considerably with speed). Their trackway II shows an undulating tail or body mark. In each of the three trackways, manus impressions can readily be distinguished from pes impressions. Overlap was reported only from trackway I.

In the Silurian to Devonian trackway of Warren *et al.* (1986), there seems to be no difference between pes and manus impressions. An average pace angulation of 99° indicates considerable speed. No overlap has been reported from this trackway. The general dimensions are comparable to the trackways of Warren & Wakefield (1972).

For a slow gait, the glenoacetabular distance L (i.e. the distance between shoulder and hips) can be estimated either graphically (Fig. 3) or using the following formula (Haubold 1984):

$$L = {}^{3}/_{4}\text{stride} + \text{distance pes–manus}$$

A distance of approximately 47 cm was calculated for the Irish trackway; graphically, the glenoacetabular distance was estimated to be 38 cm. Restorations of *Ichthyostega* (Jarvik 1980) show a ratio of total length to glenoacetabular distance of 2.5. If the same ratio is assumed for the Irish trackmaker, a body length of some 100 cm is calculated.

An '*Ichthyostega*-like animal' is considered to have made all the forementioned tracks (Warren & Wakefield 1972; Leonardi 1983; Warren *et al.* 1986). However, the Ichthyostegalians, *Ichthyostega* and *Acanthostega*, from the latest Famennian of East Greenland are distinctly younger than the trackways. New discoveries of body fossils and traces show that the tetrapods had achieved considerable specialization, high diversity and wide distribution by early Late Devonian time (Lombard & Sumida 1992 and references therein; Lebedev & Clack 1993; Ahlberg & Milner 1994). In spite of the fact that Devonian tetrapods have been known for more than 60 years, understanding of these early amphibians is still very poor. Therefore any attempt to identify the animal that made the Irish trackway would at this stage be purely speculative.

Recent research has shown that the classical picture of the earliest amphibians has to be modified (Lebedev 1990;

Table 1. *Comparison of the most important parameters of the different Devonian tetrapod trackways described in the literature.*

Reference	1	2	3	4	5	6
Locality	Australia	Australia	Australia	Australia	Brazil	Ireland
Age	Frasnian	Frasnian	Frasnian	Silurian-Early Devonian	Givetian–Frasnian	Mid-Late Devonian
Number of footprints	38	13	20	23	1	>150
Number of toes	5	?	?	?	4	?
Tail/body mark	No	Yes	No	No	–	No
Width of pace	11 cm	9.3 cm	10.5 cm	*8 cm*	–	33 cm
Stride	11 cm	17.5 cm	19 cm	19.3 cm	–	34 cm
Pace	*12 cm*	*13 cm*	*14 cm*	*13 cm*	–	35 cm
Pace angulation	53°	85°	80°	99°	–	51°
Estimated length of the animal	55 cm	?	90 cm	85.5 cm	90 cm?	1 m

1–3, Warren & Wakefield (1972); 4, Warren *et al.* (1986); 5, Leonardi (1983); 6, this paper. Italics: calculated by the author.

Bendix-Almgreen *et al.* 1990; Coates & Clack 1990, 1991; Lebedev & Clack 1993). There are two points which are of major significance for the trackways: polydactyly and palaeoecology.

The latest discoveries indicate that early tetrapods had more than five digits (*Tulerpeton*: 6 [both limbs]; *Acanthostega*: 8 [both limbs]; and *Ichthyostega*: 7 [hindlimb]; Ahlberg & Milnes 1994). These finds refute older models which postulated that pentadactyly was typical of primitive tetrapods (Jarvik 1980). Polydactyly could be responsible for the general outline of the Irish footprints which indicate very wide feet. Additionally, traces of polydactyle feet probably have a lower potential for preserving imprints of single digits.

There is strong evidence that at least several primitive amphibians (especially *Acanthostega* and *Tulerpeton*) were mainly aquatic animals (Bendix-Almgreen *et al.* 1990; Coates & Clack 1991; Lebedev 1990). This would account for the lack of tail marks in most of the Devonian trackways (supposing that the trackmaker was partially afloat in shallow water). However, it seems very unlikely that a track would be preserved in fully water-saturated sediment of this grainsize. Moreover very low body undulations are indicated by the small pace angulation in the Irish trackway. Water, however, induces a swimming motion in modern amphibians, like salamanders, with strong undulations of the body unaided by the limbs (Peabody 1959). Therefore a modern amphibian is unlikely to produce such a trackway under water. The lack of a tail mark could also be explained by a very short tail length.

The *Acanthostega* fossils from Greenland were mainly found in deposits of a meandering stream (Bendix-Almgreen *et al.* 1990) which is therefore thought to be their habitat. The Irish trackway, however, is found in an environment which was dominated by vertical accretion produced during successive floods in a non-channelized alluvial plain. It therefore seems doubtful that the track maker was a fully aquatic animal.

Conclusions

The described find is the first Devonian trackway to be positively identified in Europe. Lithostratigraphical and biostratigraphical evidence indicates a minimum age of Famennian and a maximum age of Mid-Devonian. The track maker was a primitive amphibian which lived in a fluvial environment. The animal may have had a length of approximately 1 m. It walked very slowly, as indicated by the small pace angulation. The trackway shows no morphological details except for overall outline which is probably a sign of wide feet. However nothing is known about the trackmaker itself. What it looked like, whether it resembled the Ichthyostegalian animals represented by body fossils in Upper Devonian rocks and whether it was fully aquatic (which seems unlikely) or partly or fully terrestrial are questions that still remain to be addressed.

Another trackway, although heavily weathered, was found very close to the first find, and there may be more in the surrounding area. A more detailed investigation of the bedding plane of the first find in 1994 revealed two new trackways, although these are not as extensive as the first find. An analysis of this new discovery is in preparation. Future finds may throw new light onto this poorly understood chapter in the history of terrestrial life.

I am particularly indebted to M. Ford, H. Furrer and E. A. Williams for their constant encouragement, many helpful discussions and constructive criticism of different stages in the preparation of this article. G. Leonardi has generously made available more information, partly unpublished, about early tetrapod tracks. His comments were very helpful and encouraging. Early drafts of the article were critically reviewed by Prof. D. Bernoulli, M. Ford, H. Furrer, M. Wegmann and E. A. Williams. I am grateful for their numerous suggestions and comments which have improved this contribution considerably. K. Higgs and G. Leonardi provided careful and constructive reviews. Thanks are also due to the family of E. and T. Dennehy, Cahersiveen, for their hospitality during fieldwork and to my parents as well as to W. Weibel, M. Wegmann and K. Gräfe for their spontaneous help in documenting this unexpected discovery.

Appendix: Calculation of strain

In order to calculate the bulk strain observed in the trackway, it is necessary to determine a strain ellipse on the bedding plane. The measurements (i.e. length l and orientation ϕ') of pace, stride, width of pace and of distances manus–pes plot as an ellipse-shaped distribution of points. Therefore, a best-fit ellipse has to be calculated first (least-squares ellipse; e.g. Erslev & Hongxing 1990). The parameters used in this calculation are defined on Fig. 4.

A general equation for a centered ellipse can be written as follows:

$$ax^2 + bxy + cy^2 - 1 = 0$$

a, b and c are to be calculated.

For each measurement $P = (x_p/y_p)$, which does not plot on the ellipse, a deviation q can be calculated.

$$ax_p^2 + bx_p y_p + cy_p^2 - 1 = q_p$$

In a best-fit ellipse, the sum of the squares of the deviation Q should be minimal:

$$Q = \Sigma(q^2) = \Sigma((ax^2 + bxy + cy^2 - 1)^2)$$

Q is minimal if:

$$\delta Q/\delta a = 0$$

$$\delta Q/\delta b = 0$$

$$\delta Q/\delta c = 0$$

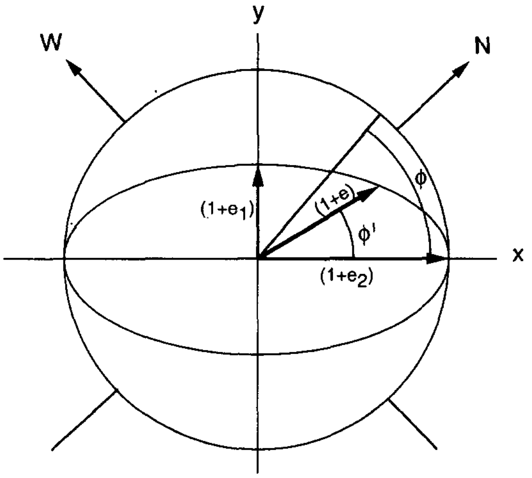

Fig. 4. Parameters used to calculate strain on bedding plane (x–y plane); x is parallel to the intersection of cleavage on the bedding plane.

These three equations allow the determination of a, b and c, i.e. the mathematical description of the strain ellipse with direction and lengths of the main axis.

Using these parameters, original length (l_0) and original orientation (ϕ) of any distance can be calculated as follows.

An ellipse with main axial lengths $(1+e_1)$ and $(1+e_2)$ can be described with the following equations (Ramsay & Huber 1983):

$$x' = (1+e_2)\cos\phi \qquad y' = (1+e_1)\sin\phi$$

or

$$x' = (1+e)\cos\phi' \qquad y' = (1+e)\sin\phi'$$

These two sets yield the expression:

$$(1+e_1)^{-2}\cos^2\phi' + (1+e_1)^{-2}\sin^2\phi' = (1+e)^{-2}$$

For the above mentioned reasons (no extension parallel to fold axis), we set: $(1+e_2)=1$.

Using these equations, it is possible to calculate the original length l_0 of l:

$$l_0(1+e) = l$$
$$l_0 = l(\sqrt{}(\cos^2\phi' + (1+e_1)^{-2}\sin^2\phi'))^{-1}.$$

References

Ahlberg, P. E. 1991. Tetrapod or near-tetrapod fossils from the Upper Devonian of Scotland. *Nature*, **354,** 298–301.

Ahlberg, P. E. & Milner, A. R. 1994. The origin and early diversification of tetrapods. *Nature*, **368,** 507–514.

Avison, M. 1984. Contemporaneous faulting, and the eruption and preservation of the Lough Guitane Volcanic Complex, Co. Kerry. *Journal of the Geological Society, London*, **141,** 501–510.

Bamford, M. L. F. & Ford, M. 1990. Flexural shear in a periclinal fold from the Irish Variscides. *Journal of Structural Geology*, **12,** 59–67.

Bendix-Almgreen, S. E., Clack, J. A. & Olsen, H. 1990. Upper Devonian tetrapod palaeoecology in the light of new discoveries in East Greenland. *Terra Nova*, **2,** 131–137.

Campbell, K. S. W. & Bell, M. W. 1977. A primitive amphibian from the late Devonian of New South Wales. *Alcheringa*, **10,** 369–381.

Capewell, J. G. 1965. The Old Red Sandstone of Slieve Mish, Co. Kerry. Proceedings of the Royal Irish Academy, **64B,** 165–174.

—— 1975. The Old Red Sandstone Group of Iveragh, Co. Kerry. *Proceedings of the Royal Irish Academy*, **75B,** 155–171.

Clack, J. A. 1988. New material of the early tetrapod Acanthostega from the Upper Devonian of East Greenland. *Palaeontology*, **31,** 699–724.

Coates, M. I. & Clack, J. A. 1990. Polydactyly in the earliest known tetrapod limbs. *Nature*, **347,** 66–68.

—— & Clack, J. A. 1991. Fish-like gills and breathing on the earliest known tetrapod. *Nature*, **352,** 234–236.

Cooper, M. A., Collins, A. D., Ford, M., Murphy, F. X., Trayner, P. M. & O'Sullivan, M. 1986. Structural evolution of the Irish Variscides. *Journal of the Geological Society, London*, **143,** 53–61.

Erslev, E. A. & Hongxing, G. 1990. Least-squares center-to-center and mean object ellipse fabric analysis. *Journal of Structural Geology*, **12,** 1047–1059.

Graham, J. R. 1983. Analysis of the Upper Devonian Munster Basin, an example of a fluvial distributary system. *International Association of Sedimentologists Special Publications*, **6,** 473–483.

Haubold, H. 1984. *Saurierfährten*. Neue Brehm Bücherei, A. Ziemsen Verlag; Wittenberg, Lutherstadt.

Higgs, K. & Russell, K. J. 1981. Upper Devonian microfloras from southeast Iveragh, County Kerry, Ireland. *Geological Society of Ireland Bulletin*, **3,** 17–50.

Horne, R. R. 1974. The lithostratigraphy of the Late Silurian to Early Carboniferous of the Dingle Peninsula, Co. Kerry. *Geological Survey of Ireland Bulletin*, **1,** 395–428.

Jarvik, E. 1955. The Oldest Tetrapods and their Forerunners. *The Scientific Monthly*, **80,** 141–154.

—— 1980. *Basic structure and evolution of vertebrates*. Academic Press, London.

Lebedev, A. O. 1984. [The first find of a Devonian tetrapod vertebrate in the U.S.S.R.] *Doklady Akademii Nauk SSSR, Palaeontology*, **278,** 1470–1473. [In Russian.]

—— 1990. *Tulerpeton*, l'animal à six doigts. *La recherche*, **225,** 1274–1275.

—— & Clack, J. A. 1993. Upper Devonian Tetrapods from Andreyevka, Tula Region, Russia. *Palaeontology*, **36,** 721–734.

Leonardi, G. 1983. *Notopus petri* nov. gen., nov. sp.: une empreinte d'amphibien du Dévonien au Paraná (Brésil). *Geobios*, **16,** 233–239.

Lombard, R. E. & Sumida, S. S. 1992. Recent Progress in Understanding Early Tetrapods. *American Zoologist*, **32,** 609–622.

O'Sullivan, M. J., Cooper, M. A., MacCarthy, I. A. J. & Forbes, W. H. 1986. The palaeoenvironment and deformation of Beaconites-like Burrows in the Old Red Sandstone at Gortnabinna, SW Ireland. *Journal of the Geological Society, London*, **143,** 897–906.

Peabody, F. E. 1959. Trackways of living and fossil salamanders. *University of California Publications in Zoology*, **63,** 1–72.

Ramsay, J. G. & Huber, M. I. 1983. *The techniques of modern structural geology; Volume 1: Strain analysis*. Academic Press Ltd, London.

Rast, N. 1983. Variscan orogeny. *In*: Hancock, P. L. (ed.) *The Variscan Fold Belt in the British Isles*. Adam Hilger, Bristol, 1–19.

Russell, K. J. 1978. Vertebrate fossils from the Iveragh Peninsula and the age of the Old Red Sandstone. *Journal of Earth Sciences, Royal Dublin Society*, **1,** 151–162.

—— 1984. *The sedimentology and palaeogeography of some Devonian sedimentary rocks in southwest Ireland*. PhD thesis, Plymouth Polytechnic.

Sarjeant, W. A. S. 1974. A history and bibliography of the study of fossil vertebrate footprints in the British Isles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **16,** i–iv + 265–378.

Stössel, I. 1993. *Die Geologie der Umgebung von Cahersiveen, Co. Kerry, Südwestirland*. Diploma Thesis, Swiss Federal Institute of Technology.

Van Veen, P. M. & Van Der Zwan, C. J. 1980. Palynological evidence concerning the Middle/Late Devonian age of the Green Sandstone Formation, McGillycuddy's Reeks, southwest Ireland. *Geologie en Mijnbouw*, **59,** 405–408.

Warren, A. A., Jupp, R. & Bolton, B. 1986. Earliest tetrapod trackway. *Alcheringa*, **10,** 183–186.

Warren, J. W. & Wakefield, N. A. 1972. Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature,* **238,** 469–470.

Westoll, T. S. 1979. Devonian fish biostratigraphy. *Special Papers in Palaeontology*, **23,** 341–353.

Williams, E. A., Bamford, M. L. F., Cooper, M. A., Edwards, H. E., Ford, M., Grant, G. G., MacCarthy, I. A. J., McAfee, A. M. & O'Sullivan, M. J. 1989. Tectonic controls and sedimentary response in the Devonian-Carboniferous Munster and South Munster basins, south-west Ireland. *In*: Arthurton, R. S., Gutteridge, P. & Nolan, S. C. (eds) *Role of Tectonics in Devonian and Carboniferous Sedimentation in the British Isles*. Occasional Publication of the Yorkshire Geological Society, 6, 123–141.

Received 24 November 1993; revised typescript accepted 1 July 1994.